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The Relationship Between Burrowing Behavior of Native Unionid Bivalves and Infestation by Zebra Mussels

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The relationship between burrowing behavior of native unionid bivalves and infestation by zebra mussels.
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BY

Amy Gries

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ABSTRACT:

Burrowing behavior of unionids was examined as a variable in colonization of unionids by juvenile zebra mussels searching for substrate. For each unionid species represented, zebra mussel densities were compared between a free-living experimental unionid and an immobilized control during each replicate. Of the four species used (*Amblema plicata*, *Quadrula quadrula*, *Leptodea fragilis* and *Obliquaria reflexa*), only *Q. quadrula* had a statistically significant difference between zebra mussel densities on the experimental mussels as compared with the controls. When zebra mussel densities on the experimental mussels were compared between species, only the comparison of *Q. quadrula* and *O. reflexa* was significantly different. *Q. quadrula* and *O. reflexa* have very different burrowing strategies but the behavior of *A. plicata* was virtually identical to that of *Q. quadrula* and yet, was not statistically different from *O. reflexa* . Other possible explanations could include shell thickness or ornamentation or some combination of any or all of the three possible explanations (thickness, ornamentation and burrowing behavior). However, neither thickness nor ornamentation can be used individually as explanations in this situation since both *Q. quadrula* and *O. reflexa* are thick-shelled and ornamented. More investigation needs to be conducted.

In the second part of the project, unionids were used as potential substrate to discover of juvenile zebra mussels would relocate from one substrate to colonize a live unionid. Four object types were used (log, aluminum beverage can, rock and empty unionid shell). In each replicate, two of the same object type with 25 zebra mussels already attached to each were placed in close proximity to a live unionid. Out of 800 zebra mussels, only one relocated to the live unionid. The other 38 that became displaced either reattached to their previous object or attached to the experimental apparatus. Unionids do not appear to be a strong enough attraction as substrate to cause attached zebra mussels to relocate.

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The zebra mussel (*Dreissena polymorpha),* a native of the Black, Caspian and Azov seas in Russia, spread throughout Europe when canals were constructed in the 1700's. It is believed that the zebra mussel was introduced into the St. Lawrence River and Great Lakes in 1986 through the expulsion of ballast water contaminated with planktonic larvae from a European freighter (Hebert, and others, 1989). The first colony of adults was discovered in Lake St. Clair in 1988 and, since that time, the zebra mussel has spread rapidly throughout the Great Lakes and many of their inland river systems including the Illinois and Ohio rivers (Griffiths and others. 1991) and most of the Mississippi.

Since the zebra mussel is an introduced species and is spreading rapidly, many biologists are conducting research to curb the deleterious effects these mussels have on aquatic ecosystems. Zebra mussels, unlike native mussels, preferentially settle and attach themselves as juveniles to hard substrates such as logs, rocks, bridges and other human-made structures, as well as on native unionid mussels (Hebert and others. 1989). Many of the human-made substrates on which zebra mussels settle (e.g. buoys, docks, boats and other floating objects) can be sunk by the weight of the settled mussels (Marsden and others, 1991). Water intake pipes used by utilities and various industries are also prime zebra mussel substrate. Zebra mussels can settle in such large densities that the inflow can be slowed, if not totally blocked. The cost to repair the damage to equipment and/or remove the mussels is usually high (Marsden and others, 1991).

Once attached, zebra mussels often relocate voluntarily in search of more suitable substrate (Marsden and others, 1991). However, it is difficult to remove this species once it has attached especially if it has colonized in large numbers. The attachment behavior of settled zebra mussels is the primary reason why zebra mussels are such a threat to

aquatic ecosystems because once introduced, they will attach to any hard substrate, and living organisms such as snails and unionid mussels are often colonized. By far, the most heavily colonized of this group are the native mussels which can be negatively affected by the zebra mussels (Marsden and others, 1991). They can compete for food because both groups are filter-feeders and zebra mussels can colonize in such quantities that the unionid is unable to open or close its shell (Personal observation). Consequently, the unionid will either be vulnerable to environment/predation (open shell) or be unable to take in oxygen or food properly (closed shell) (Mackie, 1991).

Problem statement

Native unionid mussels will naturally burrow into the soft substrate of a river or lake with its dorsal half (or less), including its siphons, exposed above the surface (Pennak 1978). Mussels do not always remain in one location however; they will occasionally burrow within the substrate. Some species remain relatively sedentary while others may move a considerable distance (1-2 meters in one hour). It has been reported that thin-shelled species tend to be more active than thick-shelled species (Pennak 1978).

Could unionid burrowing behavior play a role in influencing encounter and infestation rates by zebra mussels? Differences in burrowing activity among unionid species (depth and distance) may cause different species of unionids to be infested at different rates. Intuitively, it appears likely that species that expose more of their shells or are more sedentary would be more vulnerable to attachment by zebra mussels. Similarly, if a unionid exposes more of its shell and is sedentary, it likely becomes a larger, easier to find target

Justification

In the last few years, studies have been conducted examining substrate preferences of veliger (larval) and adult zebra mussels (Ackerman and others. 1993, Kilgour and Mackie 1993, Marsden 1993, Van Cott and others. 1993, Yankovich and Haffner 1993) and zebra mussel infestation of native unionids (Schloesser and Kovalak 1991, Hunter and Bailey 1992, Gillis and Mackie 1993, Hunter 1993, Mackie 1993, Ohnesorg and others. 1993). However, these studies did not investigate the role that unionid burrowing behavior might play in zebra mussel colonization. Nor have there been investigations on the role that unionid burrowing behavior might play in juvenile zebra mussels relocating to unionids as substrate. If unionid burrowing behavior is somehow related to zebra mussel colonization of unionids, ecologists could use this information to help explain why some mussel species are more vulnerable than others to colonization.

Purpose

The primary purpose of this investigation was: 1) to determine if differences in burrowing activities among unionid species (distance and exposure) are related to infestation by relocating juvenile zebra mussels. I hypothesized that unionid species that are more sedentary and expose more of their shells will be in greatest jeopardy of colonization by juvenile zebra mussels, and this should be particularly true at higher zebra mussel densities, and 2) to determine if zebra mussels preferentially use native mussels as substrate or if they randomly disperse over other available substrate (e. g. rocks, logs, unionids, cans).

Materials and Methods

Bivalve collection and maintenance

Between July 11 and July 13, 1994, divers collected native unionids and zebra mussels from the Illinois river. The unionid species that I used in this study included the threeridge (*Amblema plicata*), the mapleleaf (*Quadrula quadrula*), the fragile papershell (*Leptodea fragilis*), and the threehorn wartyback (*Obliquaria reflexa*).

Unionid size was standardized by selecting specimens with approximately 18 cm^2 of surface area. The threehorn wartyback was not large enough to have this amount of surface area since the largest threehorn specimens were half the size of the other three species. Only zebra mussels that were $\leq$ 20 mm long in length were used. This size class was chosen because they are more active than larger zebra mussels when searching for a suitable attachment substrate (Schloesser and Kovalak 1991). All mussels were immediately transported to the wetlab at Forbes Biological Station (Mason Co., Illinois).

Before the mussels arrived, I collected sand to be used for substrate in the various experiments from Quiver Creek, a unionid supporting stream near the Forbes lab. I sieved the sand to provide a substrate of 1 mm or smaller in particle size. Sand substrate was used because unionid mussels can burrow in it as well as or better than in gravel or mud substrates (Lewis and Riebel 1984). Furthermore, sand is also small enough in particle size to decrease the chance of zebra mussels attaching to it.

After collection, unionids were stripped of zebra mussels and byssal threads by being scraped clean with a scalpel before being placed in standard sized shallow tubs (40 cm wide X 60 cm long X 22 cm deep) with a 10 cm layer of sand substrate covered with 10

cm of water. Depths of both the sand and water were sufficiently deep enough to allow any of the mussels to completely submerge themselves within the substrate.

Mussels were maintained in a flow-through system that pumped unprocessed (i.e. unfiltered, etc.) creek water from a healthy unionid supporting creek directly into the experimental tubs via sprinkler bars; thus, all necessary requirements for mussel survival (food, oxygen, etc.) were fulfilled. Both unionids and zebra mussels were allowed to acclimate to the laboratory environment for at least two weeks before experiments were begun.

Experiment I. Unionid burrowing behavior/zebra mussel attachment

Phase 1

This phase was conducted to test the hypothesis that the behavior of the unionids might be affected by exposure to zebra mussels. Prior to zebra mussel exposure, native unionids were housed separately. The first replicate experiment was begun on July 27, 1994 and the last ended on August 22, 1994. The week before they were to be used in Phase 2 (see below), two or three unionids (1 individual from each species to be tested that week) were placed inside experimental tubs where their burrowing behaviors were recorded. Observations were recorded morning and evening for 48 hours and consisted of, 1) the amount of unionid exposed above the substrate and 2) the distance covered by each mussel since the last observation (location and trench marked on a grid and traced with a string which was then measured in cm). A match-paired t-test was conducted for each species to compare behavior before and after exposure to zebra mussels.

Phase 2

Each week, the 2-3 unionids that were used in Phase 1 were individually placed in a separate tub that was divided in half by a plexiglass wall. On either side of the wall, in the center of each half tub, a single unionid was placed. One unionid (experimental) placed on top of the sand, was free to move through the substrate. The other unionid (control) was glued to the top of a plexiglass stand at the point where the stand broke the substrate surface. This prevented any unionid movement and kept the individual in place on top of the substrate surface. A single zebra mussel was placed in each of the 25 quadrats (6 cm X 8 cm) in each half tub in order to provide a uniform distribution pattern.

Five replicate experiments were performed for each of the four native unionid species. Each experiment ran for five days. Observations were recorded morning and evening, and included 1) number of zebra mussels attached to the unionid, 2) time to first zebra mussel attachment to each unionid, 3) position of zebra mussels on the unionids (siphons, side, umbo, valve edges), 4) percentage of unionid exposed above the substrate, and 5) distance each unionid traveled in the last 12 hrs. A Chi-square test was done for each species comparing numbers of zebra mussels attached to experimental and control unionids. Chi-square tests were done comparing numbers of attached zebra mussels between species.

Experiment II. Substrate preference of zebra mussels

This experiment was conducted in order to test the hypothesis that zebra mussels prefer native unionids as substrate over other objects. I used only one mussel species, the mapleleaf (*Quadrula quadrula*), in this experiment because this species has been known to be less active and more exposed (Darin Osland, personal communication) than the

other species. Four object types were used: an aluminum beverage can (12 oz.=354 ml), a rock (granite, 5 cm X 15 cm X 4 cm), an empty unionid shell (9 cm dorsoventrally X 12 cm anterioposterially X 3 cm in height) and a log (7 cm in diameter and 15 cm long). All objects were partially buried so that the size of the exposed area of each object was similar to that of the other objects (approximately half the surface area of the aluminum can). In each half tub, I placed one mapleleaf unionid and on either side, two objects of the same type. I had allowed 25 zebra mussels to attach to each of the two objects before I added the unionids. I used previously attached zebra mussels in order to see if the species preferred a unionid substrate enough to leave their current substrate and relocate to the unionid.

Four replicate experiments for each object were conducted from August 1, 1994 to August 26, 1994. All four objects were tested each week and object types were rotated to different half tubs between replications. Observations were recorded morning and evening and included 1) zebra mussel colonization of each unionid (yes or no), 2) position of attachment, and 3) number of zebra mussels still attached to each object, 4) number of displaced zebra mussels and 5) number of zebra mussels attached to the unionid.

Results

Unionid behavior experiment

Phase 1

Comparison of experimental unionid behavior of all four species before and after the introduction of zebra mussels showed no statistically significant changes in behavior. However, a possible trend was observed in the data collected. An inverse relationship between exposure and distance for three of the four species was noted. The value of one of the variables (either distance traveled or exposure) increased while that of the other variable (distance or exposure) decreased. Although not statistically significant, the threeridge (Table 1) increased exposure from Phase 1 to Phase 2 ($\bar{X}_1$= 50.0, $\bar{X}_2$= 60.0) (matched pair t-test, tcal= -0.534, df= 4, P> 0.05), while distance was decreased ($\bar{X}_1$= 25.2, $\bar{X}_2$= 20.5) (matched pair t-test, tcal=0.256, df= 4, P> 0.05). In contrast, the mapleleaf (Table 2) decreased exposure ($\bar{X}_1$= 80.0, $\bar{X}_2$= 60.0) (matched pair t-test, tcal= 1.64, df= 4, P> 0.05) and increased distance ($\bar{X}_1$= 6.96, $\bar{X}_2$= 13.46) (matched pair t-test, tcal= -1.41, df= 4, P> 0.05).

The fragile papershell (Table 3) also increased distance ($\bar{X}_1$= 28.9, $\bar{X}_2$= 77.32) (matched pair t-test, tcal= -2.026, df= 4, P> 0.05) and decreased exposure ($\bar{X}_1$= 60.0, $\bar{X}_2$= 50.0) (matched pair t-test, tcal= 1, df= 4, P> 0.05). The only species that didn't have one factor increase while the other decreased was the threehorn wartyback (Table 4). When the distance decreased ($\bar{X}_1$= 4.32, $\bar{X}_2$= 0.54) (matched pair t-test, tcal= 1.52, df= 4, P> 0.05), exposure also decreased ($\bar{X}_1$= 60.0, $\bar{X}_2$= 0.0) (matched pair t-test, tcal= 2.45, df= 4, P> 0.05).

Phase 2

Colonization of the unionid species by zebra mussels did not appear to be affected by any particular behavior. The only species with a zebra mussel density that was significantly different between experimental and control individuals was the mapleleaf (*Quadrula quadrula*) (Table 5) (X^2cal=8.33; df=1; P<0.05). This species was fairly active and only partially exposed most of the time (Table 6). However, the threeridge (*Amblema plicata*) exhibited the same burrowing behavior as the mapleleaf but did not have significantly different zebra mussel densities between experimental and control individuals (X^2cal=0.04; df=1; P>0.05).

The other two species, fragile papershell (*Leptodea fragilis*) and threehorn wartyback (*Obliquaria reflexa),* had rather extreme burrowing strategies (Table 6). The fragile papershell was extremely active and only partially exposed the entire experimental period. The threehorn wartyback, however, was very inactive after it burrowed completely into the substrate leaving nothing exposed except the tips of the siphons. These two extremes did not have any significant effect on colonization by zebra mussels as compared to controls (fragile papershell X^2cal=1.50; df=1; P>0.05) (threehorn wartyback X^2cal=2.33; df=1; P>0.05).

When comparing the zebra mussel densities between species, only two species had densities that were significantly different from each other (the mapleleaf and the threehorn wartyback) (X^2cal=7.0; df=1; P<0.05). The threeridge exhibited the same behavior as the mapleleaf and yet was not significantly different from the threehorn wartyback. Burrowing behavior still does not appear to be the factor affecting zebra mussel density.

Thirty of the 40 unionids, experimental (16) and control (14), were originally colonized within the first 24 hrs (Table 5). There were four individuals (one experimental and three controls) that were colonized between 24-48 hrs. There were three individuals (one experimental and 2 controls) that weren't colonized for 3 or 4 days, as well as three individuals that weren't colonized at all (two experimental threehorn wartybacks and one mapleleaf control). After two days, most of the zebra mussels had found a suitable substrate (unionid, another zebra mussel or part of the tub).

There were seven incidents of a single zebra mussel being displaced from a unionid (Table 5). These incidents occurred on the three most active species: three on the threeridges, three on the mapleleafs and one on a fragile papershell. However, five of these occurred on control unionids which were fixed in position and so had nothing to do with burrowing.

The zebra mussels that colonized unionids tended to stay attached in the original contact position on the unionid. However, there was a significantly smaller number of zebra mussels attached to positions near the valve edges than were attached at either of the other three positions (Table 7) (X^2cal=8.0; df=3; $P<0.05$) with 13 out of 97 zebra mussels being located there. Of the other positions, there were 27 zebra mussels on the unionids' sides, 25 on or near the umbo and 32 near the siphons.

Substrate preference experiment

The attraction of the unionids as substrate did not appear to be great enough to attract attached or displaced zebra mussels away from the objects. Out of 800 zebra mussels, only 1 zebra mussel colonized a unionid (Table 8). It had previously become displaced

from its rock substrate and, in seeking a new substrate, colonized the unionid. The other 38 displaced zebra mussels either recolonized their original objects or attached to the tub.

Discussion

Unionid behavior experiment

Phase 1

The introduction of zebra mussels (*Dreissena polymorpha*) into the tubs containing unionids did not cause the unionids to significantly alter their behavior as compared to controls. Even though the behavior changes were insignificant, a pattern in unionid burrowing behavior was observed. This pattern resulted from the unionid burrowing method. When a unionid burrows, it pushes its foot and anterior end down into the substrate in order to obtain a hold to pull itself along horizontally. Thus, an increase in distance traveled coincided with the fact that it had to semi-bury itself in the substrate and therefore decrease exposure from phase 1 to phase 2. This pattern was demonstrated by the fragile papershell (*Leptodea fragilis*) and the mapleleaf (*Quadrula quadrula*). An increase in exposure coincided with the fact that the unionid did not travel as much and therefore remained more exposed in phase 2 than in phase 1. This was the pattern of the threeridge (*Amblema plicata*).

The threehorn wartyback (*Obliquaria reflexa*), however, decreased both distance and exposure from phase 1 to phase 2. This species burrowed vertically rather than horizontally. In other words, when it burrows, it burrows straight down until only the siphons are exposed. Thus, no distance is traveled and there is no exposure. The patterns seen in these species simply appear to be functions of their differing burrowing strategies.

Phase 2

The native unionid burrowing strategies did not appear to affect colonization of the native mussels by zebra mussels. Of the four species used (threeridge, *Amblema plicata*;

mapleleaf, *Quadrula quadrula*; fragile papershell, *Leptodea fragilis*; and threehorn wartyback, *Obliquaria reflexa*), only the mapleleaf showed a significant difference between the number of zebra mussels that colonized experimental and control mussels. It was also the mapleleaf that was significantly different from the threehorn wartyback when comparing densities between species. Behavior almost identical to that of the mapleleaf was exhibited by the threeridge and yet this species showed no significant difference. If the burrowing strategies affect zebra mussel colonization, then both of these species should have had similar results. This discrepancy could be related to the small sample sizes used in these experiments.

These same two species also had less extreme burrowing strategies than the fragile papershell which showed similar exposure but was far more active and quite different from the threehorn wartyback which was virtually unexposed and inactive. If burrowing strategies played a part in zebra mussel colonization, then these two species with more extreme burrowing strategies should have affected colonization to a much greater extent than what was observed.

This raises the question of what might have caused the difference in zebra mussel colonization of only one species (the mapleleaf) out of the four native unionids tested. If burrowing strategies did not play a role, then what did affect colonization, if anything?

Some biologists hypothesize that interspecific differences in shell thickness or morphology/ornamentation may affect the mortality rates of infested unionid mussels (Haag, and others., 1993; Schloesser, and others., 1996). Tucker and others (1993) took this a step further and thought it might be possible for shell thickness or morphology to affect actual infestation rates. However, their data did not demonstrate

any preference of zebra mussels for a particular unionid species or shell morphology. They did report that species with thin, smooth shells and species with thick, sculptured shells were both colonized by zebra mussels.

The data in my study demonstrated no difference between zebra mussel densities on thin, smooth shells as opposed to densities on thick ornamented shells either. The only two species that had zebra mussel densities that were significantly different from each other were the mapleleaf and the threehorn wartyback with the mapleleaf having 21 zebra mussels and the threehorn having 7 zebra mussels. Both species are thick-shelled and ornamented.

Tucker (1994), did a similar study in which he noted four particular patterns in which dreissenids colonized four different groups of unionid species relative to the substrate in which they burrowed. In other words, the infestation patterns were caused by the actual surface area left exposed by each unionid species as it burrowed in the substrate. In this same study, he also reported that strong evidence exists that colonization rates of unionids are related to shell thickness and ornamentation. Thin-shelled species had fewer zebra mussels per unionid than did medium-shelled species which had fewer than the thick-shelled species. His data also showed that ornate species were colonized by more zebra mussels than were species with little or no ornamentation.

The four unionid species that I used in my research fit into three of the four infestation patterns defined by Tucker (1994). The fragile papershell fell into pattern 1 which Tucker describes as colonization being confined primarily around the siphons. Both the mapleleaf and the threehorn wartyback fell into pattern three in which infestation extends a bit further and includes the siphons and the entire posterior half of

the unionid. The threeridge had infestations indicative of pattern four which was defined by one valve of the unionid having many more zebra mussels than the other. While my data did not note such patterns, it did not contradict them either. With more time, replicates and slightly differently focused observations, my data might have demonstrated these same patterns.

The mussel species used in my research demonstrated a variety of behaviors and shell morphologies and thicknesses. I have already described their different burrowing behaviors but not their shell thicknesses and morphologies. Cummings (1992) describes the mapleleaf as being thick-shelled with the lateral surface of the valves having "two rows of pustules separated by a sulcus." This species is thick-shelled and ornamented, as is the threeridge. However, the threeridge has ridges or folds only on the posterior half. There is no ornamentation anteriorly especially near the umbo (Cummings, 1992). The threehorn wartyback while thick-shelled, has large knobs that alternate from side to side (Cummings, 1992). Lastly, the fragile papershell is thin-shelled and has no ornamentation whatsoever (Cummings, 1992).

From Tucker's (1994) findings, there seems to be strong evidence that burrowing behavior as well as shell thickness and morphology are related to dreissenid infestation of unionids. My study did not take shell thickness or morphology into account. These possibly complicating factors could be one explanation for the inconclusive results received.

In addition, if time and space had allowed, I would have completed more replicates. This in itself would have given a larger data set and thus possibly a much clearer picture as to the part behavior might play in zebra mussel colonization.

In my study, burrowing behavior was tested as a potential variable preventing zebra mussel colonization of unionids. Nichols and Wilcox (1997) demonstrated that burrowing behavior can work as a means of dreissenid removal. They discovered that a temperature of 27 C and soft silt/clay sediments encourage and allow sufficient burrowing of already infested unionids to submerge themselves completely under the substrate. This action caused most if not all the zebra mussels to suffocate in the oxygen-poor sediments within 24 hours. Unionid movement in and out of the substrate also dislodged small clusters of zebra mussels that were attached to their shells. Due to the interaction of warm temperatures and soft sediments, some habitats may encourage this particular burrowing behavior and, as a result, enable unionids to clean zebra mussels from their shells when they do become infested. This indicates that some habitats could actually provide some protection from infestation for unionids. A more in depth investigation of this phenomenon would most likely provide more insight into how unionid burrowing could ultimately affect zebra mussel colonization in different habitats.

Substrate preference experiment

Several studies have been done to examine preference of dreissenids for unionid mussels as substrate. Lewandowski (1976) examined larval dreissenid substrate preferences and found that the larva (veligers) prefer to settle on unionids. Schloesser and Kovalak (1991) discovered that post-larval dreissenids, up to two years old, moved from surrounding substrates onto unionid shells. Toczylowski and Hunter (1996) found unionids (living or dead) to attract post-larval zebra mussels no more than other hard surfaces of similar size, texture and position.

The zebra mussels in my study were in the same age range as those of Schloesser and Kovalak (1991) and yet only 1 out of 800 attached zebra mussels colonized a live unionid. Once attached, they did not colonize a new substrate unless they were somehow displaced. This single individual had become displaced and, in seeking a new substrate, encountered the unionid. The unionid as a substrate may not be great enough to attract zebra mussels away from other substrates once attached.

Factors that may have played a part in these results are distance and time. The unionids were approximately 1 cm from the substrates with the attached zebra mussels. Moving the unionid into immediate proximity with the other infested substrates might have increased the chance that any unionid attraction potential would have been acted upon by the zebra mussels. Intuitively, it would seem that the greater the distance between unionid and dreissenid, the lower the possibility for the unionid to attract the experimental zebra mussels.

Time was the other factor that may have affected my results. The other studies lasted three or more months. Mine lasted only one week for each unionid tested. Perhaps the dreissenids needed a longer period of time to become attracted to the unionid. Perhaps it was a combination of both time and distance. Further work needs to be done to help sort out the possibilities.

If I were to conduct this experiment again, it would be interesting to start with unattached zebra mussels. Thus they would be free to make a choice between the unionid or the object in each replicate. If a preference is present, there would be a better chance of observing it with this setup.

In conclusion, interspecific life history differences have been postulated by various biologists as possible explanations for both differing dreissenid infestation rates of unionids and mortality rates on unionids as a result of such infestation. Burrowing behavior and/or shell thickness and morphology may all affect dreissenid infestation of unionids whether alone or in some combination. At this point, more study needs to be done to more clearly define the potential roles, if any, that these factors might have in allowing some unionid species to escape or survive infestation better than others. Substrate preference of dreissenids in both larval and post-larval stages also needs to be investigated further in order to discover if there truly is a factor that attracts zebra mussels to unionids. If answers can be found to these questions, biologists might be able to discover ways to prevent dreissenids from extirpating native unionid mussels altogether.

Table 1. Comparison of threeridge burrowing behavior in the first 48 hours of both Phase 1 and Phase 2 of Experiment I.

Replicate	Phase 1		Phase 2	
	Total distance (cm)	Exposure (%)	Total distance (cm)	Exposure (%)
1	43.1	50	97.0	100
2	6.5	50	0	50
3	9.9	50	5.5	0
4	3.8	50	0	50
5	62.8	50	0	100
	$\bar{X}$=25.2 sd=26.3	$\bar{X}$=50.0 sd= 0	$\bar{X}$=20.5 sd=42.8	$\bar{X}$=60.0 sd=41.8

Table 2. Comparison of mapleleaf burrowing behavior in the first 48 hours of both Phase 1 and Phase 2 of Experiment I.

Replicate	Phase 1		Phase 2	
	Total distance (cm)	Exposure (%)	Total distance (cm)	Exposure (%)
1	0	100	0	100
2	22.2	50	20.0	50
3	12.6	50	26.2	0
4	0	100	21.1	50
5	0	100	0	100
	$\bar{X}$=7.0 sd=10.1	$\bar{X}$=80.0 sd=27.4	$\bar{X}$=13.5 sd=12.5	$\bar{X}$=60.0 sd=41.8

Table 3. Comparison of fragile papershell burrowing behavior in the first 48 hours of both Phase 1 and Phase 2 of Experiment I.

Replicate	Phase 1		Phase 2	
	Total distance (cm)	Exposure (%)	Total distance (cm)	Exposure (%)
1	13.8	50	12.3	50
2	11.6	50	7.6	50
3	52.5	50	101.2	50
4	49.9	50	171.9	50
5	16.7	100	93.6	50
	$\bar{X}$=28.9 sd=20.5	$\bar{X}$=60.0 sd=22.4	$\bar{X}$=77.3 sd=68.7	$\bar{X}$=50.0 sd= 0

Table 4. Comparison of threehorn wartyback burrowing behavior in the first 48 hours of both Phase 1 and Phase 2 of Experiment I.

Replicate	Phase 1		Phase 2	
	Total distance (cm)	Exposure (%)	Total distance (cm)	Exposure (%)
1	0	100	0	0
2	15.0	0	2	0
3	0	100	0	0
4	6.6	0	0	0
5	0	100	0	0
	$\bar{X}$=4.3 sd=6.6	$\bar{X}$=60.0 sd=54 8	$\bar{X}$=0.5 sd=1.2	$\bar{X}$=0 sd=0

Table 6. Unionid burrowing behavior over the five day period of Phase 2 of Experiment I. (3-R= Threeridge, ML= Mapleleaf, FP= Fragile papershell, 3HW= Threehorn wartyback.)

Species	Replicate	Total distance (cm)	Exposure (%)
3-R *Amblema plicata*	1	141.8	50
	2	34.4	50
	3	5.5	50
	4	0	100
	5	0	100
ML *Quadrula quadrula*	1	0	100
	2	20.0	50
	3	26.2	50
	4	187.2	50
	5	0	100
FP *Leptodea fragilis*	1	13.7	50
	2	62.7	50
	3	101.2	50
	4	171.9	50
	5	93.6	50
3HW *Obliquaria reflexa*	1	0	0
	2	2.7	0
	3	0	0
	4	0	0
	5	0	0

Table 5. Numbers of zebra mussels attached to unionids and times of first attachment in Phase 2 of Experiment I. (3-R= Threeridge, ML= Mapleleaf, FP= Fragile papershell, 3HW= Threehorn wartyback, E= Experimental unionid, C= Control unionid, ZMA= Number of zebra mussels attached to a unionid).

Species	Replicate	ZMA (E:C)	Time (days) (E:C)
3-R *Amblema plicata*	1	3:3	1:1
	2	*1:1	1:1
	3	1:3*	.5:.5
	4	4:3	1:1
	5	3:0*	1:1
ML *Quadrula quadrula*	1	7:0	1:-
	2	4:0*	1:4
	3	*3:3	1:1
	4	3:2*	1:.5
	5	4:1	1:1
FP *Leptodea fragilis*	1	4:3*	1:1
	2	1:2	2:1
	3	1:2	3.5:1
	4	3:1	.5:3
	5	6:1	.5:1
3HW *Obliquaria reflexa*	1	3:1	1:2
	2	2:5	1:2
	3	2:1	.5:1.5
	4	0:5	-:.5
	5	0:2	-:1

*Denotes incidents of 1 displaced zebra mussel after colonization of a unionid.

Table 7. The position of zebra mussels on the unionids in Phase 2 of Experiment I. (3-R= Threeridge, ML= Mapleleaf, FP= Fragile papershell, 3HW= Threehorn wartyback, Sp= siphons, Sd= side, Um= umbo, VE= valve edges).

Species	Replicate	Experimental unionids Sp	Sd	Um	VE	Control unionids Sp	Sd	Um	VE
3-R *Amblema plicata*	1	2	-	1	-	-	2	-	1
	2	1	*1	-	-	1	-	-	-
	3	-	-	1	-	*1	3	-	-
	4	-	-	3	1	2	1	-	-
	5	-	-	1	2	-	-	*1	-
ML *Quadrula quadrula*	1	-	7	-	-	-	-	-	-
	2	1	2	1	-	*-	-	-	-
	3	*3	-	-	-	1	-	2	-
	4	-	-	3	-	-	-	*2	-
	5	-	-	4	-	-	-	1	-
FP *Leptodea fragilis*	1	3	1	-	-	-	*2	-	1
	2	-	1	-	-	-	2	-	-
	3	-	-	1	-	1	1	-	-
	4	3	-	-	-	-	-	-	1
	5	3	-	1	2	-	-	1	-
3HW *Obliquaria reflexa*	1	-	3	-	-	1	-	-	-
	2	2	-	-	-	5	-	-	-
	3	2	-	-	-	-	1	-	-
	4	-	-	-	-	-	-	-	5
	5	-	-	-	-	-	-	2	-
		20	15	16	5	12	12	9	8

*Denotes incident of one displaced zebra mussel after colonization of a unionid.

Table 8. The numbers of attached and displaced zebra mussels for each object type and unionids. (AZM= number of attached zebra mussels on each object pair, DZM= number of displaced zebra mussels from each object pair, ZMAU= number of zebra mussels attached to each unionid).

Replicate	Can AZM:DZM:ZMAU	Log AZM:DZM:ZMAU	Rock AZM:DZM:ZMAU	Shell AZM:DZM:ZMAU
1	50: 0 : 0	45: 5 : 0	41: 9 : 0	50: 0 : 0
2	45: 5 : 0	48: 2 : 0	47: 3 : 0	44: 6 : 0
3	49: 1 : 0	49: 1 : 0	48: 2 : 1	50: 0 : 0
4	48: 2 : 0	50: 0 : 0	48: 2 : 0	50: 0 : 0

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